The Distribution of Four Species of Terrestrial Amphipods (Crustacea, Amphipoda: Talitridae) on Mt. Wellington, Tasmania

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ABSTRACT

Euterrestrial amphipods were collected from the south eastern slopes of Mt. Wellington, Tasmania. Four species were present: *Talitrus vulgaris, T. tasmaniae*, an undescribed species of *Talitrus* and an undescribed species of *Orchestia*. *Talitrus vulgaris* was found most commonly in gullies and at higher altitudes. *T. tasmaniae* was commonest at lower altitudes, while *T.* sp. became dominant at the highest sites (above 1000 m). The *Orchestia* species was confined to a small area at an altitude between 1000 and 1100 m.

On a transect across a small gulley, *T. vulgaris* increased at the expense of the other two *Talitrus* spp. at the bottom of the gulley. Pitfall trapping showed that *T. vulgaris* was active at a lower level in the litter than *T. tasmaniae*. Simple temperature and humidity tolerance trials showed that *T. tasmaniae* had a higher optimum temperature than the other *Talitrus* spp. and a slightly improved humidity tolerance at 95 and 97% RH.

Although *T. vulgaris* can partially exclude the other two *Talitrus* spp. in gulleys, at many sites it coexists with them. Competition with *T. tasmaniae* is avoided by vertical separation in the litter. The basis of the coexistence with *Talitrus* sp. at high altitudes is unknown. *T. tasmaniae* appears to be an opportunistic species.

INTRODUCTION

Terrestrial amphipod crustaceans ("landhoppers") of the family Talitridae are common members of the litter fauna in the wetter forests of southern and eastern Australia, reaching very high abundances at some sites (1000 m^{-2}) (Birch and Clark, 1953; Friend and Richardson, 1977). Recent unpublished studies (Friend, 1980) have shown that the Tasmanian fauna is diverse, having at least fifteen species in seven genera.

It is common to find more than one species of landhopper at sites in Tasmania (Friend and Richardson, 1977), and preliminary investigations by the authors on the slopes of Mt. Wellington revealed that three species were present there. These three species could be found in all combinations of co-occurrence and isolation, and no pattern in their distribution was immediately obvious. The aim of this study is to describe the distribution of the landhoppers on Mt. Wellington, to elucidate as far as possible the factors limiting the distribution of each species, and to investigate the factors which permit the coexistence of species.

In order to achieve these aims, we have made an extensive survey of the distribution of landhoppers on the accessible south eastern slopes of Mt. Wellington and an intensive survey of their distribution across a forested gully. To invesigate coexistence at a site, we have used pitfall trapping to examine the possibility of vertical zonation in the soil and litter (Friend and Richardson, 1977) and we have also examined the tolerances of the species to extremes of temperature and humidity.

The taxonomy of Australian terrestrial amphipods is currently in a state of flux, pending the formal publication of a revision prepared in a thesis by Friend (1980). Two of the species found on Mt. Wellington have been described: *Talitrus tasmaniae* Ruffo 1949 and *Talitrus vulgaris* Friend 1979. Hurley (1975) has proposed subdivisions of the unsatisfactorily large genus *Talitrus* into eight subgenera. Using Hurley's scheme the two named species and the remaining unnamed one can be more fully classified as *Talitrus* (*Mysticotalitrus*) *tasmaniae, Talitrus* (*Mysticotalitrus*) sp. and *Talitrus* (*Keratroides*) *vulgaris.* In the interests of brevity, the subgeneric names will not be used further here. During the course of the study, a further species, in the genus *Orchestia,* was collected. It is also included in Friend's (1980) revision, but must be referred to as *Orchestia* sp. here. Voucher specimens of all the species recognised in this study have been deposited in the Tasmanian Museum and Art Gallery, Hobart (Museum Numbers G2734-G2747 inclusive).

Sites

Mt. Wellington (1270 m) is the highest point of a block of high ground lying immediately to the west of the River Derwent. This block, produced by faulting, consists of sedimentary Permian and Triassic rocks overlain by a 350 m thick sill of Jurassic dolerite. Mountains of this form are common in south eastern Tasmania.

The soils of Mt. Wellington have been described by Martin (1940). Briefly, they consist of peaty High Moor and Skeletal soils on the summit plateau and upper slopes, and Podsols below 800 m. At higher altitudes, where erosion proceeds faster than weathering, boulder fields occur.

Although substantially colder than Hobart, the climate of Mt. Wellington is relatively mild. Average daily maximum and minimum temperatures at the summit range from 1.1 to 7.3°C, with an extreme range from about -6 to 30°C (Bureau of Meteorology, 1975), and although snow may fall in any month, severe frosts are uncommon (Richardson, unpublished data). Annual rainfall ranges from 700 mm on the lower slopes, to over 1400 mm at the summit, and the region above 600 m is frequently covered with cloud. The south eastern slopes, where this study was carried out, are substantially shaded in winter.

The vegetation of the mountain has been described by Martin (1940) and Ratkowsky and Ratkowsky (1977), who proposed seven and twelve vegetation groups, respectively. For the purposes of this study, only five vegetation types were recognised. Arranged in ascending altitude, these were: (1) Gully Associations. These were dominated by *Bedfordia salicina, Pomaderris apetala, Olearia argophylla* and *Dicksonia antarctica. Atherosperma moschatum* was common in some gullies. Although small shrubs were absent, ground cover was provided by the ferns *Blechnum wattsii* and *Polystichum proliferum.* Occasional *Acacia dealbata* were present in some gullies. The main components of the litter were leaves of *D. antarctica, B. salicina* and *O. argophylla. P. apetala* was less conspicuous in the litter as its leaves tend to decompose to a large extent before falling. The gullies had a rich, dark brown soil and a denser canopy than surrounding areas.

(2) *Eucalyptus obliqua* Associations. The main forest tree at lower altitudes was *E. obliqua* with an understorey of the three gully species (*O. argophylla, B. salicina* and *P. apetala*), combined with tall shrubs such as *Phebalium squameum, Zieria arborescens, Acacia verniciflua, Oxylobium ellipticum* and *Pultenaea juniperina.* These areas tended to have many fallen tree trunks, around which litter was built up off the ground to a depth of 30-60 cm. The litter was mostly eucalypt leaves and bark. The canopy was less dense than in the gullies and the soil was poorer and stonier.

(3) *Eucalyptus urnigera, E. johnstonii, E. delegatensis* Associations. At the upper limit of the *E. obliqua* association, a noticeable change in terrain occurred, with boulder fields becoming common, especially at higher altitudes. In these areas *E. urnigera, E. johnstonii* and *E. delegatensis,* and to a lesser extent *E. coccifera,* dominated. The understorey species were smaller and sparser than in the *E. obliqua* association with species such as *Hakea lissosperma, Pimelea nivea, Cyathodes dealbata, Pultenaea juniperina* and *Ghania psittacorum* dominating. The litter was predominantly eucalypt, built up thinly on top of the rocks. The canopy cover was further reduced and the soils were very stony.

(4) *Eucalyptus coccifera* Associations. At altitudes above 1000 m this was the dominant association. The ground cover was generally low (up to 30 cm), while in sheltered areas, shrubs up to 2 m developed, but *E. coccifera* was the only species of any height. Other species in this association included *Bauera rubioides, Coprosma nitida, Orites revoluta, Astelia alpina, Celmisia* sp. and *Poa* sp. There was no general build up of litter, but *E. coccifera* leaves tended to settle at the bases of the trees and between rocks. Canopy cover was less than in the other associations.

(5) Montane Shrubbery Associations. This association was confined to the highest altitudes (above 1200 m) on the summit plateau. Eucalypts were entirely

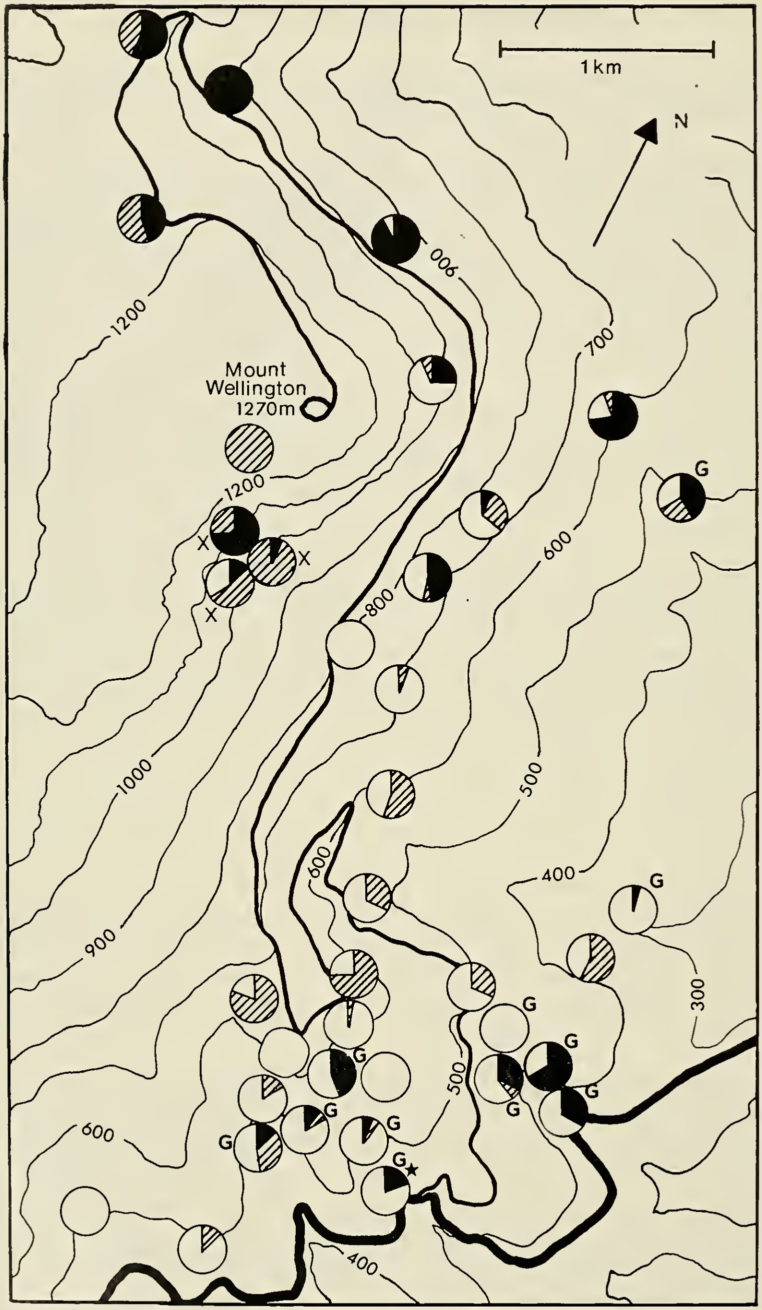

Fig. 1. The relative abundances of terrestrial amphipods found at 37 sites on Mt. Wellington. Sites classified as gullies are marked G. The Fern Glade intensive study site is marked with an asterisk. Solid: *Talitrus vulgaris;* cross-hatched: *Talitrus* sp.; open: *Talitrus tasmaniae;* cross: *Orchestia* sp. (presence only).

absent and the tallest vegetation was a shrubbery (up to 1 m) consisting principally of *O. revoluta* and *Richea scoparia*. Much of the ground was bare rock or herbfield. There was only an occasional build up of litter where the tallest shrubs prevented the growth of ground layer plants.

All of these vegetation zones have been severely affected by fire at one time or another. The most recent fire to affect the whole area was in 1967, and much of the vegetation is regrowth from that time.

METHODS

Extensive Survey

Sites were sampled in two series, the first between August and October, 1980, the second in March 1981. In the first series, the litter from ten 625 cm^2 quadrats was collected from each site, while in the second, five quadrats of the same size were sampled at most sites. At the highest altitudes, the very rocky terrain and sparse vegetation resulted in such small amounts of litter that quadrat sampling was no longer appropriate, and such litter as could be found was collected by hand.

The litter was sorted by hand in a tray on the site and the amphipods were removed with an aspirator, preserved in 70% alcohol, and later identified in the laboratory.

The sites were classified into one of the five classes described above.

Intensive Survey

A 140 m transect line was set up across the Fern Glade gully (Fig. 1), running approximately east-west. Amphipods were sampled at 10 m intervals along the transect, ten 625 cm^2 quadrats being taken at each station. The following parameters of the habitat were measured at each station: the moisture content of the soil and litter (weight loss after 50 h drying at 105°C); soil organic content (estimated as the weight lost after ignition at 450°C for 4 h); canopy cover, as estimated by the hemispherical photographic technique of Anderson (1964); litter depth (an average of three measurements at each site); and soil pH as measured by a CSIRO soil pH test kit.

Pitfall Trapping

Twenty-four pitfall traps were set up at each of three sites, one in the Fern Glade gully (F2) and two in the Jackson's Bend gulley (J3 and J5). These sites, all of which were in gully vegetation associations, were chosen for their high densities of animals. Eight traps were placed at three different levels in the litter, that is, with the lip of the trap (1) level with the soil surface, (2) at the soil litter interface, and (3) approximately four centimetres below this interface. Quadrat samples for comparison with trap results were taken within the vicinity of the traps to determine the proportion of amphipod species in the litter. Between August and October 1980, the traps were left for up to 36 days, or until a sufficient number of animals had accumulated.

The traps consisted of a plastic drinking cup of 7 cm diameter, protected from rain by a plastic Petri dish lid supported 50 mm above it on wooden legs. Those traps set below the litter surface were surrounded by plastic netting (mesh size 10 x 9 mm) which protruded above the soil surface and prevented debris from falling into the trap, while allowing unhindered access to the traps by the amphipods. Saturated aqueous picric acid was used as an odourless preservative.

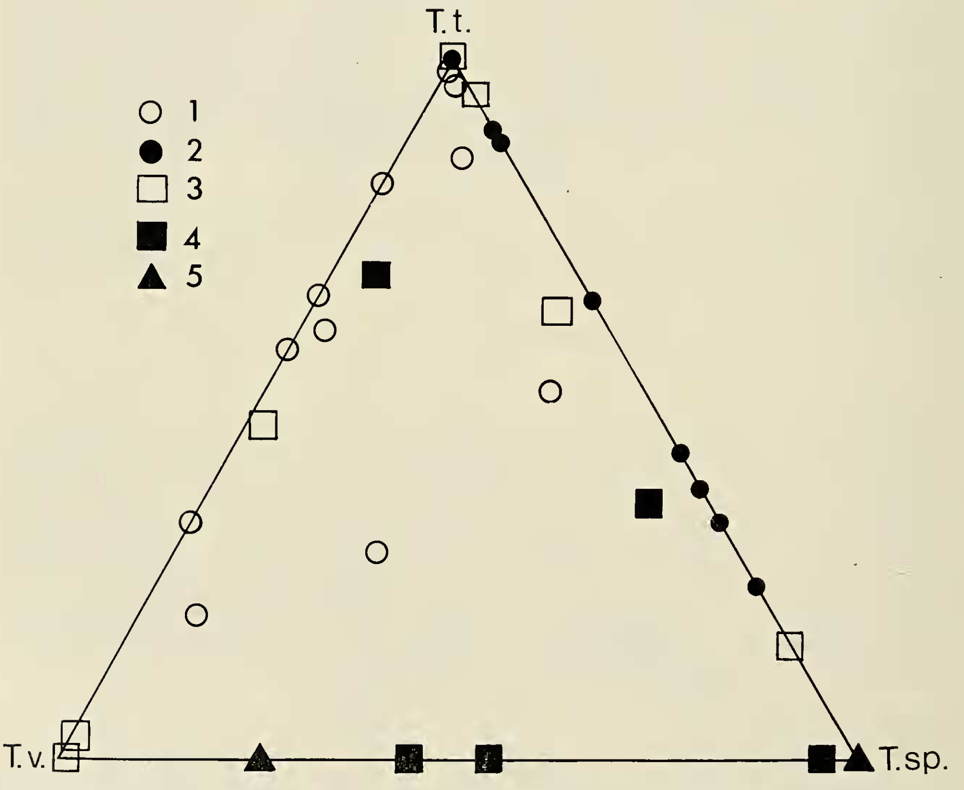

Fig. 2. Ternary Diagram showing the relative abundances of the three major species in the five habitat types recognised. The apices of the triangle represent 100% of each species. T.v.: *Talitrus vulgaris;* T. sp.: *Talitrus* sp.; T.t.: *Talitrus tasmaniae.* 1: Gully Associations; 2: *Eucalyptus obliqua* Associations; 3: *Eucalyptus urnigera, E. johnstonii, E. delegatensis* Associations; 4: *Eucalyptus coccifera* Associations; 5: Montane Shrubbery.

Tolerance Experiments

These were performed in chambers consisting of a plastic Petri dish with its base replaced by a fine nylon mesh, placed on the top of a similar dish containing a solution of KOH appropriate to the required humidity (Solomon, 1952). When the animals had been placed in the dish, a lid was taped onto the upper chamber. The animals were provided with food in the form of small pieces of leaves.

Temperature tolerances were tested at 100% relative humidity, using temperatures of 0°C, 5°C, 10°C, 15°C, 18°C, and 23°C. Groups of animals were acclimated at 5°C and 15°C before the experiment for 5 days. At least 20 animals of each species were used in each trial.

The humidity trials were carried out at 15°C, using 10 animals which had been acclimated at 15°C and 100% RH. Trials were carried out at 97%, 95%, 93%, 90%, 85% and 80% RH. The chambers were checked at regular intervals and the number of deaths noted.

RESULTS

During the study, five specimens of a fourth species of amphipod were collected from a very localised area immediately to the south of the Organ Pipes formation, at an altitude of between 1000 and 1100 m.

The proportions of species found at the sites examined during the extensive survey are shown in Figure 1. The number of animals collected at each site ranged from 8 to 366, but over 75% of samples contained more than 50 animals. While *Orchestia* sp. is very limited in its distribution, the other three species are found at almost all altitudes, but there is a substantial amount of variation in their proportions at the various sites. *Talitrus tasmaniae* is more prominent at the low altitude sites (i.e. below 800 m), while *Talitrus* sp. becomes dominant at the very highest sites. *Talitrus vulgaris* shows evidence of a discontinuous altitudinal distribution, being prominent both at low altitudes (below 500 m) and at high altitude (above 900 m).

Figure 2 shows the relative abundances of the three species plotted on a ternary diagram. The sites are distinguished on the basis of their vegetation. Few sites show anything approaching equal proportions of the three species, indeed only 10 out of the 37 sites contain all three species. One clear trend emerges from the vegetation records: The complete absence of *Talitrus vulgaris* from *Eucalyptus obliqua* associations. This is reflected in its under-representation from intermediate altitudes, where *E. obliqua* is the dominant tree. *T. tasmaniae* is absent from montane shrubbery, reflecting its absence from high altitudes; and from many gulley sites, but there are no other clear trends in the relationships between the proportions of amphipod species and vegetation type.

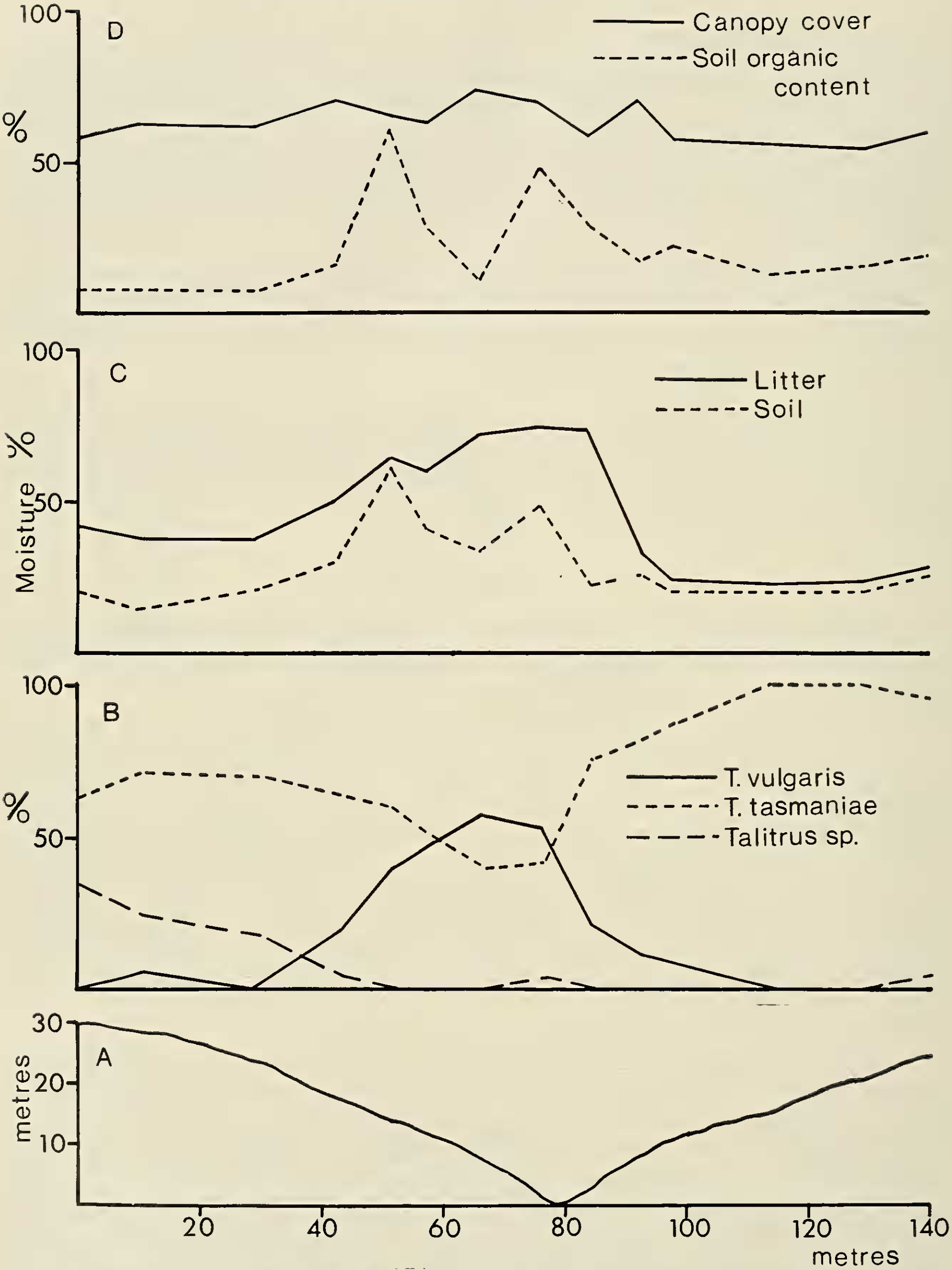

Fig. 3. Amphipod abundances and variation in physical parameters across the gully transect. A: profile of the gully; B: relative abundances (%) of the amphipod species; C: variation in litter and soil moisture; D: variation in canopy cover and soil organic content.

Figure 3 shows the relative abundances of the three species on the gully transect, and the physical factors measured along it. *Talitrus vulgaris* clearly increases in the bottom of the gully, while *T. tasmaniae* and *Talitrus* sp. both decline. *T. tasmaniae* is much commoner on the western side of the gully.

Of the physical factors measured, soil and litter moisture content increase in the gully. Soil organic content reaches much higher values in the gully than on the slopes, although it varies considerably in the gully. There is a barely discernable decline in canopy cover at either end of the transect. Neither pH nor litter depth showed any systematic variation and have not been included on the figure.

TABLE 1. Frequencies of the three amphipod species captured in pitfall traps at three levels (Level 1: surface; Level 2: soil-litter interface; Level 3: 3-4 cm below soil-litter interface) at three sites: F2, J5, J3. The frequencies of the three species in quadrat samples taken at the same sites are also given. Figures in brackets are percentages. The chi-squared values compare the frequencies at each level with those from the quadrat samples. ***: $P<0.005$; **: $0.01>P>0.005$; n.s.: not significant.

		Talitrus tasmaniae	*Talitrus* sp.	*Talitrus vulgaris*	Chi-squared
F2	Level 1	86 (95)	2 (2)	3 (3)	0.04 n.s.
	Level 2	108 (94)	3 (3)	4 (3)	0.28 n.s.
	Level 3	88 (92)	2 (2)	6 (6)	2.25 n.s.
	Quadrat	134 (95)	4 (2.5)	3 (2.5)	
J5	Level 1	120 (92)	1 (1)	9 (7)	12.17 ***
	Level 2	102 (83)	2 (2)	18 (15)	1.56 n.s.
	Level 3	92 (77)	2 (1)	26 (22)	0.39 n.s.
	Quadrat	252 (79)	6 (2)	61 (19)	
J3	Level 1	52 (95)	—	3 (5)	10.37 **
	Level 2	82 (91)	—	8 (9)	11.27 ***
	Level 3	70 (76)	—	22 (24)	0.0004 n.s.
	Quadrat	131 (76)	—	55 (24)	

The results of the pitfall trapping are shown in Table 1. The catches from each of eight traps at the three depths have been amalgamated, and the proportions of species observed in the quadrat samples have been included for each site. The departure of the observed frequencies of species caught at each level from those in the quadrat samples were tested using chi-squared, and the results are included in the table. At site F2, none of the catches at any of the three depths differs from the overall proportion in the litter, but the numbers of *T. vulgaris* and *Talitrus* sp. are both low.

At site J5, the catch at the upper level contains more *T. tasmaniae* than expected, and fewer *T. vulgaris,* while the catch at the two lower levels does not differ from that in the quadrat sample.

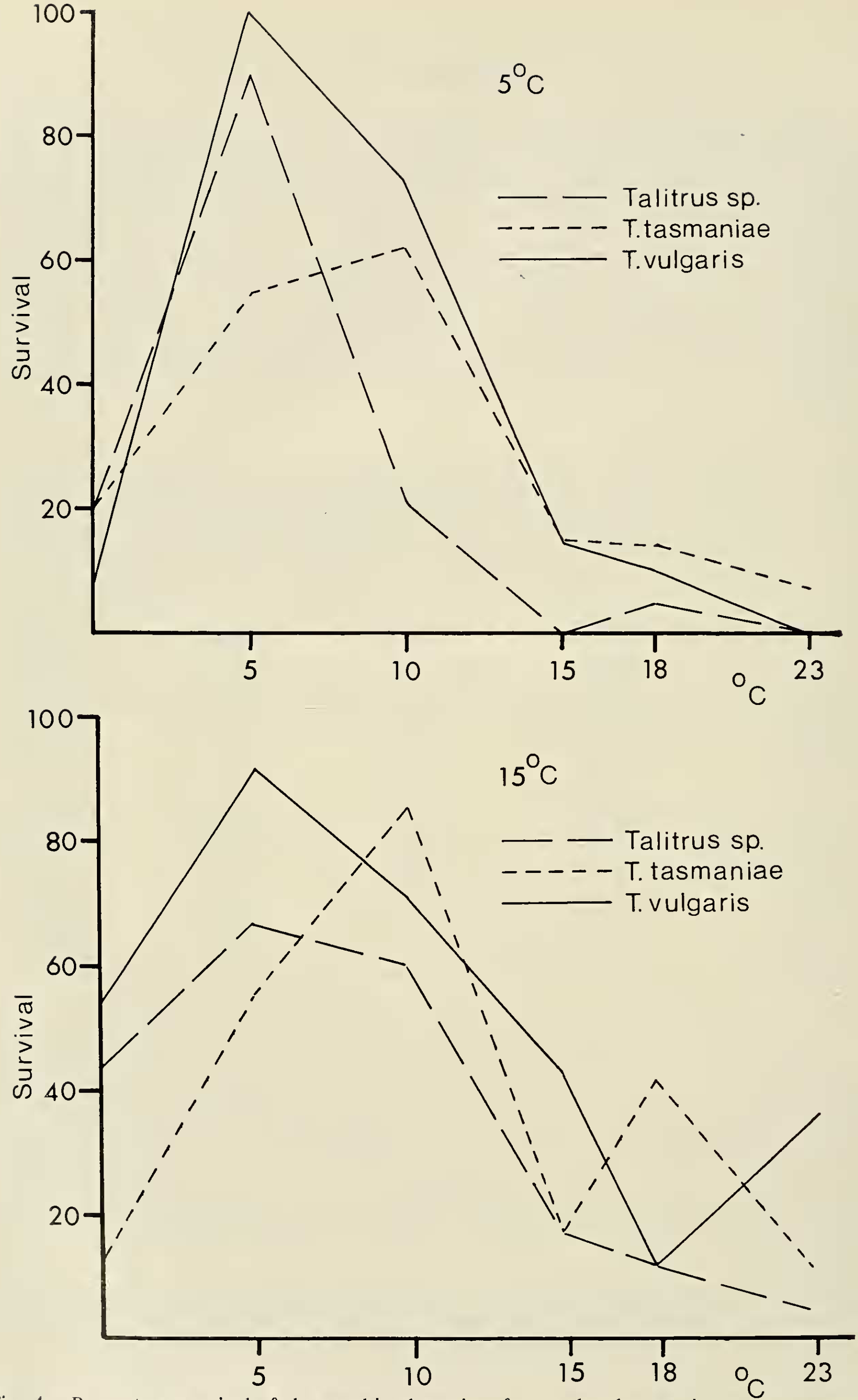

Fig. 4. Percentage survival of the amphipod species after twelve days at six test temperatures. The animals were acclimated to either 5° or 15°C.

At site J3, the upper level catch also departs from the expected in the same way as at J5, and the same departure can be seen at the intermediate level, while the catch at the lower level resembles the quadrat sample once again.

It appears that *T. tasmaniae* is more active on the surface and in the upper layers than *T. vulgaris,* and this is apparently due to a vertical separation between the species, rather than differential activity, since the lowest level catch always reflects the overall litter proportions. If *T. vulgaris* were simply less active, and hence trapped less often, the lowest catch should reflect this as well as the upper ones.

In order to summarise the results of the temperature tolerance experiments, the percentage of survivors after 12 days exposure to the six test temperatures is plotted in Figure 4, for each acclimation temperature. At both acclimation

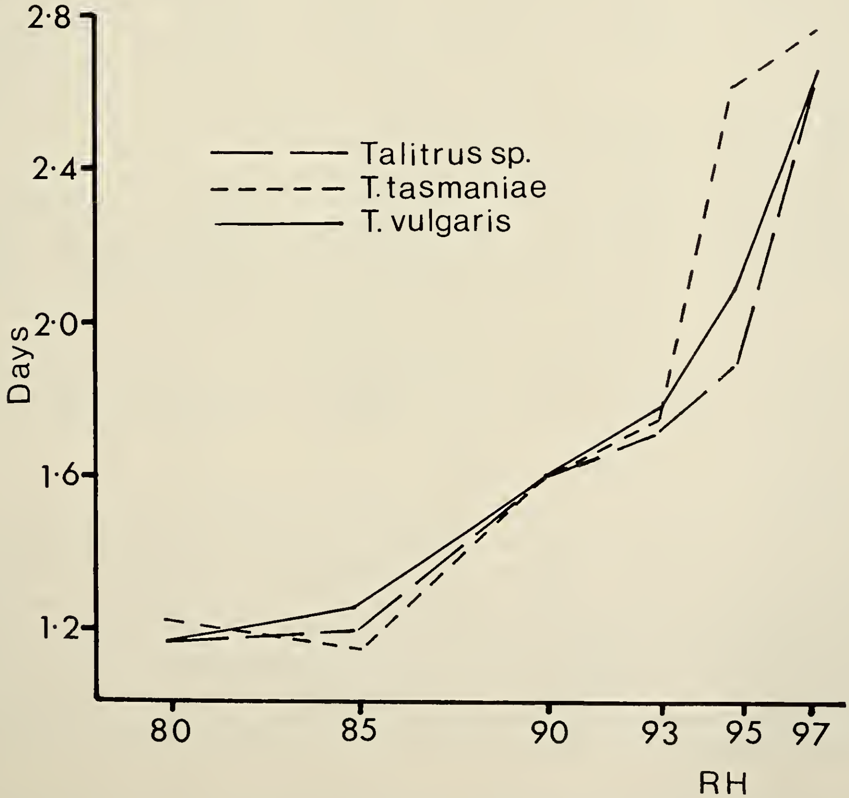

Fig. 5. Days required to produce 50% mortality of the three amphipod species at six test humidities. The tests were performed at 15°C.

temperatures, *T. vulgaris* and *Talitrus* sp. have their highest survival at 5°C. *T. tasmaniae* shows a higher optimum, 10°C, in both cases. The tolerance ranges of all three species are broadened after acclimation to 15°C and this is particularly marked in *Talitrus* sp.

Figure 5 shows the results of the humidity tolerance trials. Average survival declines sharply with decreasing humidity, and there is very little variation between the three species, apart from a suggestion of improved survival in *T. tasmaniae* at 95 and 97% relative humidity.

DISCUSSION

Although the distributional data collected here show no discrete differences between the three major species, there is circumstantial evidence to suggest how their distributions are controlled, and how they partition the available space when they coexist. Thus *Talitrus tasmaniae* is found most extensively at lower altitudes, where it is presumably able to colonise habitats not available to the other two species through its better tolerance of higher temperature (and there is also a suggestion that it has an improved tolerance to lower humidity), *Talitrus vulgaris* is most prominent in gullies and at high altitudes, which corresponds to its higher tolerance to cool conditions compared to *T. tasmaniae.*

Little can be seen in the data to separate *Talitrus* sp. from *T. vulgaris.* Its numbers decline sharply in the face of increasing numbers of *T. vulgaris* across the gully transect, and so, in the absence of any evidence from the tolerance experiments, it could be concluded that this is the result of competitive exclusion by *T. vulgaris.* However, at the higher altitudes, *Talitrus* sp. coexists with *T. vulgaris,* so in that situation, the latter's competitive ability has apparently been lost. It is worth noting that these observations have been made over relatively short periods of time, at a restricted time of year. It is possible that the proportions of species change from season to season as changes in the climate alter the balance of advantage from one species to another.

Talitrus tasmaniae is more active on the litter surface than are the other species, which is supported by the indication that it has better tolerance of high temperatures and lower humidities. It is possible that *T. tasmaniae* is an opportunistic, fugitive species (*sensu* Hutchinson, 1951), colonising new areas and eventually being outcompeted in them, except where its wider tolerances allow it to colonise areas unavailable to other species. Further evidence, in the form of long-term data on the changes in proportion of the species at a single site, and also on the distances moved by individuals of the various species, is needed to test this hypothesis.

Among the classical correlates of r-selected species are found small body size and high reproductive potential (Pianka, 1970). In terrestrial amphipods, these trends may be obscured because a) larger body size enables the female to brood larger numbers of eggs, thus enhancing her reproductive potential, and b) larger size implies both a larger reservoir of water and a smaller surface area in relation to volume. Thus in these animals, large body size may be advantageous to a mobile species, within certain limits, and be associated with an increased reproductive potential. The upper limit to body size is likely to be set quite low by the animal's need to be able to find shelter in small spaces and crevices in the soil and litter.

Since no direct evidence of competitive exclusion can be presented here, some consideration must be given to the possible mechanisms which allow the species to coexist. Friend and Richardson (1977) investigated the coexistence between *Talitrus vulgaris* and a species not present on Mt. Wellington, *Talitrus* (*Keratroides*) *angulosus.* They suggested that there was a vertical separation between the two species, with *T. vulgaris* predominating in the upper and surface layers. *T. angulosus,* which is smaller, unpigmented and has reduced eyes and appendages, was found in the lower layers of the litter and in the soil. Friend and Richardson (1977) suggested that this separation was maintained by competition for space.

In that case, *T. vulgaris* was the upper litter species, whereas on Mt. Wellington, it is found in the lower layers, with *T. tasmaniae* above. However, while *T. angulosus* shows obvious adaptations to burrowing (pigmentation, length of appendages and body size), *T. vulgaris* and *T. tasmaniae* are superficially similar in those characteristics. It will be of interest to investigate the vertical separation in a site where all three species (*T. tasmaniae, T. vulgaris* and *T. angulosus*) occur together. Such sites have been recorded by Friend (1980), in Tasmania.

Examples of other soil macroarthropods which separate vertically in the soil and litter are given by Wallwork (1976). There is no evidence at present for any dietary separation in the niches of Tasmanian amphipods (Friend and Richardson, 1977; Friend, 1980).

Information on the geographical distribution of the three *Talitrus* species in Tasmania is given by Friend (1980). *Talitrus vulgaris* is the most widespread Tasmanian landhopper, occurring throughout the state. *T. tasmaniae* is the most restricted species of the three studied here, occurring only in the south east. *Talitrus* sp. has the same range as the latter, plus an extension into the west and south west. The very extensive distribution of *T. vulgaris* is paradoxical in view of its restricted distribution on Mt. Wellington. Friend (1980) makes no comment on the habitat preferences of this species, but notes that there are several forms within the species which may qualify for species rank. Differences in the tolerances of these forms may account for the restricted distribution observed here.

Because of its very restricted range, the discussion above has ignored the occurrence of the *Orchestia* sp. recorded for the first time on Mt. Wellington in this study. This record extends the range of the species compared with Friend's (1980) records. The nearest previous records were from the Snowy Range at altitudes of 6-900 m, some 50 km south west of Mt. Wellington. This species of *Orchestia* might be expected on other outliers of the west and south west highlands, such as the Mt. Field massif and Wyld's Craig.

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